

Feeding Asian pangolins: An assessment of current diets fed in institutions worldwide

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Pangolins are ant specialists which are under intense threat from the illegal wildlife trade. Nutrition has notoriously been their downfall in captivity and is still an issue in regards to rescue and rehabilitation. We analyzed the nutrient content of diets used by institutions that are successfully keeping Asian pangolins and to assess the variety of the ingredients and nutrients, compared these with the nutritional requirements of potential nutritional model species. We performed intake studies at five institutions and also had data from three other institutions. We also analyzed five different wild food items to use as a proxy of wild diet. We observed two categories of captive diets: those mostly or completely composed of insects and those high in commercial feeds or animal meat. Nutrient values were broad and there was no clear rule. The non-protein energy to protein energy ratio of the diets were much higher than the wild food items, more so for those which receive less insects. The average contribution of carbohydrate, fat, and protein energy were also further away from the wild samples the less insects they contained. The previously suggested nutritional model for pangolins is the domestic dog which is supported by our relatively large nutrient ranges of apparently successful diets, however, due to their highly carnivorous nature; the upper most nutrient intake data are not consistent with this and favor the feline nutrient recommendations. We are unable to render a conclusion of what model is more appropriate based on our data collected.

KEYWORDS

ants, chitin, insectivore, myrmecophagy, nutritional geometry

1 | INTRODUCTION

Pangolins are myrmecophagous mammals of the order Pholidota, divided into two groups: Asian and African. There are eight species of pangolin, four of which are found in Africa (all listed as Vulnerable by the IUCN) and four in Asia: Sunda (*M. javanica*) and Chinese (*M. pentadactyla*), both listed as Critically Endangered, and Philippine (*M. culionensis*) and Indian (*M. craussicaudata*), both endangered (Batin & Widmann, 2008; Hoffmann, 2008a, 2008b, 2008c, 2008d; Molur, 2008). Numbers of all pangolin species have been reduced significantly due to extensive hunting for their scales, which are used in Asian traditional medicine even though there is a lack of evidence on its efficacy, and their meat which is considered a delicacy in countries such as China and Vietnam (Mahmood, Hussain, Irshad, Akrim, & Nadeem, 2012). The Sunda and Chinese pangolins are

particularly at risk and ways to protect them in situ are thus far feeble (Challender et al., 2014a, 2014b).

Wild population figures for Asian pangolins are rough estimates at best, although they range over much of Southeast Asia (IUCN, 2008). It is believed that high levels of hunting have resulted in a decrease of 80% in the wild over the last 15 years for Asian species and that this decline will continue as hunting spreads throughout the species range (Challender et al., 2014a). At present, pangolins are believed to be the most heavily trafficked wild mammal globally. When confiscations do occur, the pangolins are in a negative health and welfare state (Pattnaik, 2008). They are living through psychological stress and suffer many different types of physical wounds, including damage to the digestive tracts which originate either from traders pumping silt and cement into pangolins to make them heavier and, therefore, fetch a higher price or from gastric ulcers from not having eaten for an extended

period of time (Nguyen, pers. comm.). On rare occasions when live confiscated animals are received at rescue centers, common practice is to release them as quickly as possible because 67% of all captive pangolins are reported to die within the period of 10 days after arrival, with more succumbing to malnutrition thereafter (Mohapatra & Panda, 2014). The major causes of death are physical injuries and stress but if they can be kept alive initially, nutrition is reported to be a major issue (Yang et al., 2007). Their diet is thought of as very specific, termites and ants, yet very little information exists on the species ingested and their nutrient intake (Lim & Ng, 2008). Ants are difficult to source for Asian rescue centers and zoos, especially in quantities large enough to feed a group of confiscated pangolins arriving at short notice, which also explains why so few zoos worldwide exhibit pangolins (Challender, Thai, Jones, & May, 2012). The difficult transition from a wild ant diet to a captive “gruel” type diet and little knowledge to their nutritional requirements is also why providing adequate nutrition is the biggest hurdle in their captive husbandry (Lissa, 1988; Yang et al., 2007). Investigating an easily accepted, nutritionally appropriate diet for pangolins has wide reaching effects: engaging the education capabilities of zoos by holding pangolins in their collection, improving rescue and rehabilitation success rates and furthering our understanding on the use of model species for advising exotic animal nutrition.

Nutrient requirements of wild animal species are largely unknown and how they are fed is based on a “model” species for which there is already an understanding of their nutritional needs. Often domestic models such as dogs (Bellanger et al., 2015), cats (Vester et al., 2010), swine (Tajima & Aminov, 2015), poultry (Wilkinson, Bradbury, Thomson, Bedford, & Cowieson, 2014), rat (Robbins, 2012), horse (Hagen et al., 2015; Johnson, 2014), rhesus macaque (O’Sullivan et al., 2013), duck (Robbins, 2012), mink (Diez-Leon & Mason, 2016), goat (Weiss, Schook, & Wolfe, 2014), and sheep (Gattiker et al., 2014) are used. Choice of model species will depend on phylogenetic relatedness, similarity in feeding ecology and/or digestive morphology and physiology. When it comes to the Pangolin, the giant anteater (*Myrmecophaga tridactyla*) would appear the valid choice due to similarities in feeding ecology (Redford, 1985) and it is the most studied among the myrmecophagous mammals (McNab, 1984). The requirements for the giant anteater are generally based on the nutritional model of the domestic dog. For this reason, we aim to characterize the nutritional composition of successfully managed pangolin diets across eight successful institutions and discuss the appropriateness of nutritional models.

2 | MATERIALS AND METHODS

2.1 | Diet analysis

We collected diet information from Wildlife Reserves Singapore (WRS-Singapore), Ragunan Zoo (Indonesia), Save Vietnam's Wildlife (SVW-Vietnam), Taipei Zoo (Taiwan), Ueno Zoo (Japan), Leipzig Zoo (Germany), Nandankanan Zoo (India), and Chongqing Normal University (China). The total study population included 29 pangolins (Table 1). We personally conducted intake studies at WRS, SVW, Taipei, Ueno, and

TABLE 1 The study population for each institution

Location	Common name	Scientific name	Study population (n = m.f.u.)
WRS	Sunda Pangolin	<i>M. javanicus</i>	2.2.0
SVW	Sunda Pangolin	<i>M. javanicus</i>	4.7.0
Ragunan	Sunda Pangolin	<i>M. javanicus</i>	-
Chongqing	Sunda Pangolin	<i>M. javanicus</i>	-
Taipei	Chinese Pangolin	<i>M. pentadactyla</i>	3.7.0
Ueno	Chinese Pangolin	<i>M. pentadactyla</i>	1.1.0
Leipzig	Chinese Pangolin	<i>M. pentadactyla</i>	1.1.0
Nandankanan	Indian Pangolin	<i>M. crassicaudata</i>	-

WRS, Wildlife Reserves Singapore; SVW, Save Vietnam's Wildlife.

Leipzig, however, limited data were available from Ragunan and the data from Nandankanan zoo and Chongqing were obtained from Mohapatra et al. (2013) and Yu, Jiang, Peng, Yin, & Ma (2015), respectively. We defined the diets used at these institutions as “successful” due to their diets supporting longevity (institutions keeping pangolins alive for more than 5 years) and health (no deaths within the last 5 years).

2.2 | Intake analysis

We observed the diet preparation of each institution's long-term diets for 7 days with each ingredient being weighed individually before being mixed together into a gruel-type mix which made delivery and intake easy to quantify. We weighed the total amount of food given to each pangolin, as well as the amount of uneaten food. The amount of uneaten food was adjusted for desiccation (as described in Das et al., 2015) and subtracted from the amount offered to result in a food ingested value. If we were unable to weigh any animals during the study period, we used their most recent weights provided by the institution. The pangolins at SVW were kept as wild as possible pending release and not handled, therefore no weights were available.

2.3 | Nutrient analysis

We sent every food item to a nutrition laboratory within each respective country for direct nutrient analysis using the methods described in Norconk and Conklin-Brittain (2004) for proximate analysis. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) were analyzed as per Van Soest (1994). Water soluble carbohydrates (WSC) and energy were calculated as estimates since laboratory analyses were not available in each country. WSC were calculated as in Johnson, Raubenheimer, Rothman, Clarke, & Swedell (2013) by subtracting ash, crude protein, crude fat, and NDF from total dry matter. Digestible energy was calculated using the standard values of 4 kcal/g for crude protein and carbohydrates, and 9 kcal/g for crude fat. We collected five nests of green weaver ants near SVW in Vietnam, totaling 1,536 g of ant matter. We analyzed a whole nest with its proportions of adults, eggs and larvae; and the following two samples analyzed were only adults and also a combination of larvae and eggs. In addition, we purchased black ants at a local bird market

and analyzed one sample of only adults, and one sample of black ant larvae with eggs. These were also sent for nutrient analysis using the same laboratory methods as the previously mentioned food samples.

2.4 | Data analysis

We compared the daily diet intake amounts per individual across the five institutions using a Kruskal–Wallis tests. We used the nutritional geometric framework (Simpson, Raubenheimer, Behmer, Whitworth, & Wright, 2002) to graph the ratio of protein energy in kcal (PE) versus non-protein energy in kcal (NPE) ingested. Macronutrient balancing is best analyzed with comparable units, usually energy, and is pertaining to protein/non-protein energy as necessary nutrient requirements (Johnson et al., 2016). Each axis represents a nutrient (*y*-axis is PE and *x*-axis is NPE, both in kcal) and the graph is the nutrient space. Food items have mixtures of PE and NPE and thus may be represented as lines drawn out from the origin into the nutrient space at angles dictated by their internal ratio of nutrients contained within that food. The pangolins could not change route within nutrient space without switching to another food (Simpson & Raubenheimer, 1999).

We used the relative proportions of crude fat to crude protein to soluble carbohydrates in a right mixture triangle analysis such as Johnson et al. (2013), along with the result of the five native ant samples to observe differences between captive diets and native food items to compare the daily contribution of nutrients to energy versus wild food types.

3 | RESULTS

Food types used include invertebrates (ants, red weaver ants, green weaver ants, weaver ant eggs (unspecified), red ants, bee larvae, silk worms, and/or mealworms), vertebrates (beef meat, eggs, and/or egg yolks), plant matter (coconut husk, apples, corn flour, and/or soya beans), concentrates (cat pellets, hedgehog pellets, and/or insectivore pellets), dairy (yogurt), and supplements (clay, chitin powder, calcium lactate, vitamin B, vitamin A, vitamin K, choline chloride, carbomin-SVM, and/or olive oil) (Table 2). We did not present exact amounts of specific ingredients to discourage replication in pangolin farming trials, however, proportions of ingredients and nutrient intakes should be sufficient to inform animal managers. There was a high variability in

nutrient content of the diets across institutions: crude fat ranged from 18.56% to 31.37%, crude protein from 32.41% to 55.11%, ADF from 4.61% to 16.01%, NDF from 9.12% to 18.94%, Ca 0.15% to 1.27%, P from 0.23% to 0.84%, and WSC from 1.6% to 25.84% (Table 3). There was a significant difference in total dry matter intake per species of pangolin ($X^2_{(4)} = 22.20$, $p = 0.001$). The Sunda pangolins on average ingested more dry matter than their Chinese counterparts (Table 4).

The majority of captive diets had substantially higher proportions of soluble carbohydrate, lower protein, and similar levels of crude fat than the wild ant samples (Figure 1). The Sunda pangolin diets were somewhat closer in composition to the wild ant samples than the Chinese pangolin diets, which can be visually assessed in the Right-Angled Triangle analysis. Sunda diets were also closer to the nutritional space occupied by wild ant samples than Chinese diets in terms of NPE/PE ingested. The non-protein energy was larger in all captive diets which was the main difference with wild-type ratios (Figure 2). The diets made largely of invertebrates have ratios more similar to the wild ant nutritional space. The nutritional geometric framework did not identify any obvious intake targets or rules of compromise.

5 | DISCUSSION

Captive Asian pangolins were fed gruel-type diets made with a variety of ingredients including invertebrates, meat, plant matter, concentrated pellets, and supplements which naturally results in a large range of nutrient concentrations. All the diets in this study were deemed successful by their respective institution using them (proven longevity, no diet-related chronic health issues except some overweight individuals, breeding, and mother rearing at a few institutions); therefore pangolins may not have very specific nutrient requirements. The diets appear successful despite differing in the proportions of macronutrients and the ratio of protein to non-protein energy from those observed in five samples of wild food items (Figures 1 and 2). There is no information available on pangolin NPE/PE intake in the wild. The NPE/PE ratios of ant species were used as a proxy for wild pangolin diets and currently is the closest approximation, ranging between 0.48:1 and 1.2:1. Nutrition involves a lot more than a simple NPE/PE ratios, however, this method allows us to visualize and compare major macronutrients of the diets such as (Droscher, Rothman, Ganzhorn, & Kappeler 2016), after which,

TABLE 2 Proportion of each diet ingredient category as fed, for the different institutions holding pangolins

	WRS	Ragunan	SVW	Taipei	Ueno	Leipzig	Nandankannan	Chongqing
Invertebrates	55.8	100	100	53.1	24.3	46.4	60	88
Vertebrates	38.5	-	-	4.3	10.9	3.3	40	-
Plant Matter	-	-	-	28.8	24.4	23.5	-	12
Concentrate	2.1	-	-	3.3	14.6	-	-	-
Dairy	-	-	-	-	1.5	-	-	-
Supplements	3.6	-	-	10.5	24.3	6.7	-	-
Water	-	-	-	-	-	21.1	-	-

Invertebrate ingredients used: mealworms, silkworm larvae, weaver ants, red ants, and bee larvae. Vertebrate ingredients used: hard-boiled egg, egg yolk, beef meat, and horse meat.

TABLE 3 Nutrient concentrations of each institution's diets on a dry matter basis and the results of weaver and black ant nutrient analysis with cat and dog requirements for comparison

	Ash (%)	Crude fat (%)	Crude protein (%)	ADF (%)	NDF (%)	Ca (%)	P (%)	WSC (%)	DM (%)
WRS	6.415	27.334	52.58	10.17	12.09	0.22	0.25	1.581	79.99
Ragunan	5.65	24.63	50.86	9.76	15.80	0.15	0.83	3.06	-
SVW	4.33	31.27	53.68	8.86	9.12	0.25	0.67	1.6	55.5
Taipei	5.06	18.56	36.7	14.63	15.49	0.84	0.84	24.19	51.52
Ueno	4.8	27.51	32.41	4.61	9.44	0.94	0.67	25.84	72.2
Leipzig	6.56	23.82	32.69	9.137	15.34	1.27	0.366	21.59	21.27
Nadakannan ^a	2.52	20.13	55.11	-	-	-	-	-	-
Chongqing ^b	3.01	28.65	37.11	16.01	18.94	-	-	12.29	47.23
Average	7.42	23.99	43.88	10.11	13.32	0.62	0.59	14.60	54.62
S.D. (±)	6.23	5.74	10.00	3.99	3.53	0.46	0.23	10.09	20.64
W. ant nest	5.61	25.75	51.84	11.93	14.28	0.16	0.62	2.52	70.2
W. ant adults	5.92	16.29	65.09	9.23	11.79	0.34	0.88	0.91	77.45
W. ant larvae	6.65	14.63	50.76	7.37	12.83	0.2	0.73	15.13	60.72
B. ant adults	4.38	16.12	51.68	16.19	26.54	0.33	0.69	1.28	79.66
B. ant larvae	6.88	21.7	49.86	9.98	16.47	0.3	0.73	5.09	63.18
Dog ^d		5	18.0 ^c			1	0.8		
Cat ^d		9	23			1	0.8		

WRS, Wildlife Reserves Singapore; SVW, Save Vietnam's Wildlife; ADF, acid detergent fiber; NDF, neutral detergent fiber; WSC, water soluble carbohydrate; DM, dry matter; W. ant, weaver ant nest (entire nest contents), adults (only adults, all castes), larvae (mix of larva and eggs); B. ant, black ant adults (adults only) and larvae (larvae and eggs).

^aData modified from Mohapatra et al. (2013).

^bData modified from Yu et al. (2015).

^cRequirements range from 17% to 22% depending on quality of the protein 5, 19, 20.

^dDog and cat requirements were obtained from NRC (2006) and updated by Case et al. (2011).

other nutrients can then be assessed. Due to the large variance observed in nutrients, each should be individually mentioned.

5.1 | Protein and amino acids

The most studied related species successfully kept in captivity is the giant anteater whose nutritional requirements have been modeled after those of the domestic dog (Gull et al., 2015). This was suggested due to the anteater's capability of producing the amino acid taurine from sulphur amino acids, a metabolic pathway also available to dogs. Two of the Sunda pangolin groups were fed diets consisting entirely of invertebrates, SVW and Ragunan. The average taurine content of feeder insects is 0.57 g/kg of insect protein as is (±0.52) which is a low value (beef has an average value of 5.1 g/kg of protein) (Finke 2013, 2015). Individuals at both of these sites have either bred and reared their own pups, or arrived pregnant and reared their own pups

TABLE 4 Average dry matter (DM) intake for both Sunda and Chinese pangolins at the five institutions where intake studies occurred

	Sunda	Chinese
Weight ingested (g)	60.28	53.88
SD (±g)	22.47567	15.59
Average weight (kg)	7.36	5.00
Moisture in diet (%)	64.70	64.95

successfully on these insect only low taurine diets. This supports the conclusions of Gull et al. (2015). Insects can be a good source of methionine (mean value of 3.16 ± 1.15 g/kg of insects as is) and of cysteine (1.35 ± 0.32 g/kg of insects as is) which we can assume meets the requirements of the Sunda pangolins to endogenously produce sufficient amounts of taurine (Finke 2013, 2015).

Average protein content of the diets was 43.88% DM which ranged from as low as 32.41–55.11% (Table 3). The mean value is

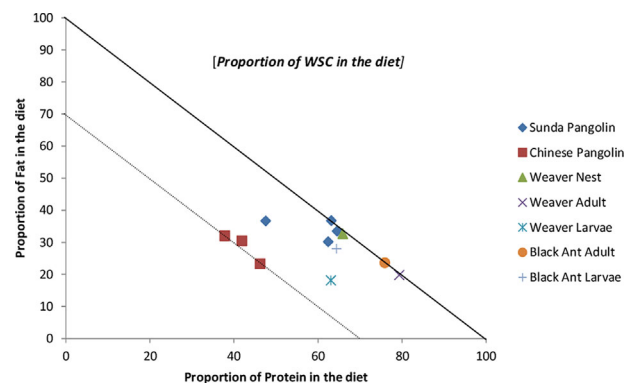


FIGURE 1 A right mixture triangle plot representing the proportion of protein to fat to water soluble carbohydrates (WSC) on a dry matter basis in each diet and in five ant samples known to be consumed by wild Sunda pangolins. The implicit axis is proportion of WSC; the hard black line represents 0% soluble carbohydrates and the dotted line represents 30%

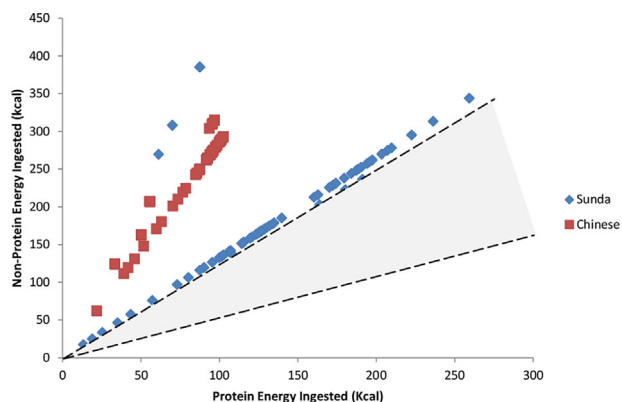


FIGURE 2 Macronutrient balance of protein versus non-protein energy (in kcal) for daily pangolin intake values in five institutions where the diamonds represent *M. javanicus* and the squares represent *M. pentadactyla*. Dashed rails indicate the nutritional rails of the most nutritionally extreme wild food items. The gray space demarcates the bounds of nutritional space of the potential macronutrient balances available to wild pangolins consuming these food items in any proportion, therefore the shaded area demarcates nutritional space where we estimate wild pangolins to be

much higher than the recommendations for adult cats or dogs based on (Case, Daristotle, Hayek, & Raasch, 2013) and NRC (2006). Native ant foods had an average concentration of 53.85% crude protein and termites have an average of 58.20% (Oyarzun, Crawshaw, & Valdes, 1996). Half of the diets came near the proportion of crude protein in the diet that is similar to ant species, with Sunda pangolin diets being closer than the Chinese pangolin diets (Figure 1). Similarly, the Sunda diets had a larger invertebrate and vertebrate content within their diet. Even though wild food items of pangolins appear to be high in protein, this does not necessarily reflect a high requirement as diets as low as 32.41% led to maintenance. Wild pangolins presumably also ingest some amount of soil or leaf matter while foraging in ant nests which would dilute their overall protein intake (Lim & Ng, 2008). Protein energy was also underrepresented in all of the diets, which are all much higher in lipid and carbohydrate energy. Gruel-type diets are ideal for nutritional geometry studies as the animals have no choice but to ingest the ratio of dietary ingredients that is prepared for them. Only when multiple mixes with different ratios are available to them can we then determine intake targets or rules of compromise, such as prioritizing protein over carbohydrate intake or vice versa (Simpson & Raubenheimer, 2012). Lissa (1988) gave two captive Chinese pangolins the option of a diet made with silkworm larvae or one meat-based formula and the latter was chosen most often. This study did not include nutrient content of the diets; therefore a conclusion is difficult to extrapolate, especially as taste preference may have been a factor. The dog or cat model do not fit the current pangolin diets although the higher protein requirements of the carnivorous cat is closer to the pangolin diets surveyed in this study.

5.2 | Fats and carbohydrates

Average crude fat contents of the diets were 23.99% DM (± 5.74) with a range of 18.56–31.27% (Table 3). The average value was higher than the recommendations for domestic dogs and cats. The higher fat content

required for cats may be a better fit for the pangolins as the native insect preys of pangolins have a mean crude fat content of 18.89%. The proportions of crude fat in the diet are also more constant and less variable than the proportion of protein, made obvious by the lack of vertical movement in Figure 1. Crude fat is necessary for many metabolic pathways but is also a main source of energy for insectivores, which are general low in WSC (ant nest average is 2.52%). Diets were much higher in WSC than the ant average (average of 14.60%, range from 1.6 to 25.84%), yet this appears to be in spite of protein and not fat content. Soluble carbohydrates are not the natural energy source of felines, however, they are able to digest them efficiently (Kienzle, 1993). Similarly, our data support that pangolins are also able to use soluble carbohydrates as a source of energy. If such a high proportion of the pangolin's diet was not absorbable, we would have observed emaciated individuals within the Chinese pangolins whose diets were higher in WSC than the Sunda. These were the populations where overweight individuals were observed, but this may be due to other factors discussed later. The tendency to create pangolin diets with a high NPE/PE ratio may not be detrimental per se, as they may be able to use soluble carbohydrates and fats interchangeably as energy, being consistent with the canid nutritional model (Figure 2).

5.3 | Other factors to consider

Sunda pangolins were heavier than the Chinese in this study (7.36 vs. 5.00 kg) which is reflective of wild weights as well (Lim & Ng, 2008). Their intake rates were variable; however, on average Sunda pangolins consumed 6.40 g more. The slight difference between intake rates does not scale with the 2.36 kg difference between average body weights, suggesting some individuals are overweight. The average moisture content of the gruel diet was 45.38% and ranged from 21.01 to 78.73% with the higher moisture contents being fed to Chinese Pangolins. Weight management in gruel-type diets should be relatively straight forward by manipulating the water content of feeds, therefore diluting energy, controlling the amounts given, and even providing lots of non-digestible carbohydrates or sand/earth to dilute the energy even further which mimics their wild feeding ecology (Lim & Ng, 2008). In addition, perhaps the Chinese pangolins were simply fed too large of a quantity, which may have no reflection on the nutritional content of their diets. Diets which contained a higher amount of chitin may have increased apparent organic matter digestibility due to the larger food mean retention time associated with more chitinous diets (Chin et al., 2009). This may help the nutritional management of rescued pangolins which require critical care and a sustained nutrient intake, assuming they find the diet palatable. Although insects are dense in energy, their high chitin content reduces the total available energy in a full stomach, and the high earth content consumed also takes up space and further dilutes the energy on an as is basis.

It was consensus among authors to not provide the quantification of ingredients for each diet to discourage pangolin farming. Common sense may dictate that farming an animal which is heavily used in the wildlife trade would directly reduce their poaching pressure. This link is not supported by any evidence, in fact quite the opposite. Farming tigers and bears in China for tiger parts and bear bile, respectively, created a niche market, raising the price of "premium wild" products which placed

further pressure on the wild populations (Dutton, Hepburn, & Macdonald, 2011; Nowell, 2000). Simply making a link between farmed and wild resources does not realistically model the market in terms of consumer demand dynamics. In spite of this, we were able to present sufficient information for future comparisons on pangolin and other captive myrmecophagous diets.

5.4 | Nutrient ranges of studied diets

Due to the nature of the data we collected, we are only able to comment on the range of apparently successful diets, not on nutrient recommendations, compared with the nutrient compositions of some wild foods. Crude protein was between 30 and 55%, crude fat 15 and 30%, ADF 7 and 16%, calcium 0.25 and 1.0%, and phosphorous 0.20 and 0.80%, and WSC should be kept as low as possible, below 25%. The pangolin diets are not consistent with the nutrient requirements of neither cats nor dogs. The larger fat and protein levels and low WSC values are closer to the values of the carnivorous cat, rather than the omnivorous dog. Their taurine requirements, however, may be more related to the dog. Also, the general large variation between nutrient contents of the diets is also consistent with the canid physiological model (Careau, Morand-Ferron, & Thomas, 2007). Pangolins may require the nutrients of a carnivore, however, they may be able to cope with/adapt to certain variations of nutrient intake. For micronutrients, we would recommend using the feline carnivorous values until more evidence surfaces on pangolin physiology. Using one model does not fit pangolins requirements fully, especially from domesticated animals with a vastly different feeding niche (Mahmood, Jabeen, Hussain, & Kayani, 2013). Similarly with the case of a herbivorous giant panda (*Ailuropoda melanoleuca*), nutrient recommendations must be adapted and drawn from many sources, as one mould cannot fit all (Dierenfeld, Qiu, Mainka, & Liu, 1995).

6 | CONCLUSION

1. The macronutrient requirements of pangolins may be broader than expected as we observed a large variation in nutrient contents among eight diets.
2. With our current understanding of pangolin physiology and morphology and the data presented in this paper, we cannot determine which physiological model is more appropriate for the pangolin. It is also possible that neither are appropriate.
3. The NPE/PE ratio of zoo diets was much higher than that of wild diets.
4. Future research should concentrate on understanding if pangolins target a specific NPE/PE intake ratio.

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REFERENCES

- Batin, G., & Widmann, P. (2008). *Manis culionensis*. IUCN Red List of Threatened Species. Version 2013.1. Available online at: <http://www.iucnredlist.org/details/136497/0>.
- Bellanger, S., Benrezzak, O., Battista, M. C., Naimi, F., Labbe, S. M., Frisch, F., & Baillargeon, J. P. (2015). Experimental dog model for assessment of fasting and postprandial fatty acid metabolism: pitfalls and feasibility. *Laboratory Animals*, *49*, 228–240.
- Careau, V., Morand-Ferron, J., & Thomas, D. (2007). Basal metabolic rate of canidae from hot deserts to cold Arctic climates. *Journal of Mammalogy*, *88*, 394–400.
- Case, L. P., Daristotle, L., Hayek, M. G., & Raasch, M. F. (2013). *Canine and feline nutrition: a resource for companion animal professionals* (3rd ed.). Maryland Heights, MI: Mosby Inc.
- Challender, D. W. S., Thai, N. V., Jones, M., & May, L. (2012). Time budgets and activity patterns of captive Sunda pangolins (*Manis javanica*). *Zoo Biology*, *31*, 206–218.
- Challender, D., Baillie, J., Ades, G., Kaspal, P., Chan, B., Khatiwada, A., ... Hsieh, H. (2014). *Manis pentadactyla*. The IUCN Red List of Threatened Species. Available online at: www.iucnredlist.org.
- Challender, D., Nguyen, V. T., Shepherd, C., Krishnasamy, K., Wang, A., Lee, B., ... Chung, Y. (2014). *Manis javanica*. The IUCN Red List of Threatened Species. Version 2014.3. Available online at: www.iucnredlist.org.
- Chin, S. C., Yang, C. W., Lien, C. Y., Chen, C. L., Guo, J. C., Wang, H. T., & Yeh, L. S. (2009). The effect of soil addition to the diet formula on the digestive function of Formosan pangolin (*Manis pentadactyla pentadactyla*). Asian Meeting on Zoo and Wildlife Medicine/Conservation Proceedings: Seoul.
- Das, A., Smith, M., Saini, M., Katole, S., Kullu, S. S., Gupta, B. K., ... Swarup, D. (2015). Effect of concentrates restriction on feed consumption, diet digestibility, and nitrogen utilization in captive Asian elephants (*Elephas maximus*). *Zoo Biology*, *34*, 60–70.
- Diez-Leon, M., & Mason, G. (2016). Effects of environmental enrichment and stereotypic behaviour on maternal behaviour and infant viability in a model carnivore, the American mink (*Neovison vison*). *Zoo Biology*, *35*, 19–28.
- Dierenfeld, E. S., Qiu, X., Mainka, S. A., & Liu, W. X. (1995) Giant panda diet fed in five Chinese facilities: an assessment. *Zoo Biology*, *14*, 211–222.
- Droscher, I., Rothman, J. M., Ganzhorn, J. U., & Kappeler, P. M. (2016). Nutritional consequences of folivory in a small-bodied lemur (*Lepilemur leucopus*): effects of season and reproduction on nutrient balancing. *American Journal of Primatology*, *160*, 197–207.
- Dutton, A. J., Hepburn, C., & Macdonald, D. W. (2011). A stated preference investigation into the Chinese demand for farmed vs. wild bear bile. *PLOS ONE*, *6*(7), e21243. doi: 10.1371/journal.pone.0021243
- Finke, M. D. (2013). Complete nutrient content of four species of feeder insects. *Zoo Biology*, *32*, 27–36.
- Finke, M. D. (2015). Complete nutrient content of four species of commercially available feeder insects fed enhanced diets during growth. *Zoo Biology*, *34*, 27–36.
- Gattiker, C., Espie, I., Kotze, A., Lane, E. P., Codron, D., & Clauss, M. (2014). Diets and diet-related disorders in captive ruminants at the national zoological gardens of South Africa. *Zoo Biology*, *33*, 426–432.
- Gull, J. M., Stahl, M., Osmann, C., Ortmann, S., Kreuzer, M., Hatt, J. M., & Clauss, M. (2015). Digestive physiology of captive giant anteaters (*Myrmecophaga tridactyla*): determinants of faecal dry matter content. *Journal of Animal Physiology and Animal Nutrition*, *99*, 565–576.
- Hagen, K., Müller, D. W., Wibbelt, G., Ochs, A., Hatt, J. M., & Clauss, M. (2015). The macroscopic intestinal anatomy of a lowland tapir (*Tapirus terrestris*). *European Journal of Wildlife Research*, *61*, 171–176.

- Hoffmann, M. (2008a). *Phataginus tricuspis*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. Available online at: <http://www.iucnredlist.org/details/12767/0>.
- Hoffmann, M. (2008b). *Smutsia gigantea*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. Available online at: <http://www.iucnredlist.org/details/12762/0>.
- Hoffmann, M. (2008c). *Smutsia temminckii*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. Available online at: <http://www.iucnredlist.org/details/12765/0>.
- Hoffmann, M. (2008d). *Uromanis tetradactyla*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. Available online at: <http://www.iucnredlist.org/details/12766/0>.
- IUCN. (2008). IUCN Red List of Threatened Species. Available online at: <http://www.iucnredlist.org>.
- Johnson, N. F. (2014). Characterization of Grape Condensed Tannins and their Effect on Black Rhinoceros (*Diceros bicornis*) Hindgut Fermentation. Doctoral dissertation, University of Missouri.
- Johnson, C. A., Raubenheimer, D., Rothman, J. M., Clarke, D., & Swedell, L. (2013). 30 Days in the life: daily nutrient balancing in a wild Chacma Baboon. *PLoS ONE*, 8, e70383.
- Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J., & Rothman, J. M. (2016). Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). *American Journal of Primatology* (in press).
- Kienzle, E. (1993). Carbohydrate metabolism of the cat. 3. Digestion of sugars. *Journal of Animal Physiology and Animal Nutrition*, 69, 203–210.
- Lim, N., & Ng, P. (2008). Home range, activity cycle and natal den usage of a female Sunda pangolin *Manis javanica* (Mammalia: Pholidota) in Singapore. *Endangered Species Research*, 4, 233–240.
- Lissa, E. (1988). Biology, husbandry, and veterinary care of captive Chinese pangolins (*Manis pentadactyla*). *Zoo Biology*, 7, 293–312.
- Mahmood, T., Hussain, R., Irshad, N., Akrim, F., & Nadeem, M. S. (2012). Illegal mass killing of Indian pangolin (*Manis crassicaudata*) in Potohar region, Pakistan. *Pakistan Journal of Zoology*, 44, 1457–1461.
- Mahmood, T., Jabeen, K., Hussain, I., & Kayani, A. R. (2013). Plant species association, burrow characteristics and the diet of the Indian pangolin, *Manis crassicaudata*, in the Potohar plateau, Pakistan. *Pakistan Journal of Zoology*, 45, 1533–1539.
- McNab, B. K. (1984). Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology*, 203, 485–510.
- Mohapatra, R. K., Panda, S., Sahu, S. K., Roy, P. K., Purohit, K. L., & Mishra, C. R. (2013). Hand-rearing of rescued Indian pangolin (*Manis crassicaudata*) at Nandankanan zoological park, Odisha. *Indian Zoo Yearbook*, 7, 17–25.
- Mohapatra, R. K., & Panda, S. (2014). Husbandry, behaviour and conservation breeding of Indian pangolin. *Folia Zoologica*, 63, 73–80.
- Molur, S. (2008). *Manis crassicaudata*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. Available online at: <http://www.iucnredlist.org/details/12761/0>.
- National Research Council (NRC). (2006). *Nutrient requirements of dogs and cats*. Washington: National Academies Press.
- Norconk, M. S., & Conklin-Brittain, N. L. (2004). Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology*, 25, 1–26.
- Nowell, K. (2000). *Far from a cure: the tiger trade revisited*. Cambridge: Traffic.
- O'Sullivan, A., He, X., McNiven, E. M., Hinde, K., Haggarty, N. W., Lönnnerdal, B., & Slupsky, C. M. (2013). Metabolomic phenotyping validates the infant rhesus monkey as a model of human infant metabolism. *Journal of Pediatric Gastroenterology and Nutrition*, 56, 355–363.
- Oyarzun, S. E., Crawshaw, G. J., & Valdes, E. V. (1996). Nutrition of the Tamandua: I. Nutrient composition of termites (*Nasutitermes spp.*) and stomach contents from wild tamanduas (*Tamandua tetradactyla*). *Zoo Biology*, 15, 509–524.
- Pattnaik, A. K. (2008). Enclosure design and enrichment key to the successful conservation breeding of Indian pangolin (*Manis crassicaudata*) in captivity. *Indian Zoo Yearbook*, 5, 91–102.
- Redford, K. H. (1985). Feeding and food preference in captive and wild giant anteaters (*Myrmecophaga tridactyla*). *Journal of Zoology*, 205, 559–572. Cambridge, NY: Academic Press.
- Robbins, C. (2012). *Wildlife feeding and nutrition* (pp. 14–152). Cambridge, MA: Academic Press.
- Simpson, J. S., & Raubenheimer, D. (2012). *The nature of nutrition: a unifying framework from animal adaptation to human obesity* (pp. 21–79). Princeton, NJ: Princeton University Press.
- Simpson, S. J., & Raubenheimer, D. (1999). Assuaging nutritional complexity: a geometrical approach. *Proceedings of the Nutrition Society*, 58, 779–789.
- Simpson, S. J., Raubenheimer, D., Behmer, S. T., Whitworth, A., & Wright, G. A. (2002). A comparison of nutritional regulation in solitary and gregarious-phase nymphs of the desert locust *Schistocerca gregaria*. *Journal of Experimental Biology*, 205, 121–129.
- Tajima, K., & Aminov, R. (2015). *Structure and function of a nonruminant gut: a porcine model. In rumen microbiology: from evolution to revolution* (pp. 47–75). New Delhi, India: Springer India.
- Van Soest, P. J. (1994). *Nutritional ecology of the ruminant*. Ithaca, NY: Cornell University Press.
- Vester, B. M., Burke, S. L., Liu, K. J., Dikeman, C. L., Simmons, L. G., & Swanson, K. S. (2010). Influence of feeding raw or extruded feline diets on nutrient digestibility and nitrogen metabolism of African wildcats (*Felis lybica*). *Zoo Biology*, 29, 676–686.
- Weiss, R. B., Schook, M. W., & Wolfe, B. A. (2014). Long-acting neuroleptic use for reproductive management of non-domestic ungulates using the domestic goat (*Capra hircus*) as a model. *Zoo Biology*, 33, 204–211.
- Wilkinson, S. J., Bradbury, E. J., Thomson, P. C., Bedford, M. R., & Cowieson, A. J. (2014). Nutritional geometry of calcium and phosphorous nutrition in broiler chicks: the effect of different dietary calcium and phosphorous concentrations and ratios on nutrient digestibility. *Animal*, 8, 1080–1088.
- Yang, C. E., Chen, S., Chang, C. Y., Lin, M. F., Block, E., Lorenstein, R., ... Dierenfeld, E. S. (2007). History and dietary husbandry of pangolins in captivity. *Zoo Biology*, 26, 223–230.
- Yu, J., Jiang, F., Peng, J., Yin, X., & Ma, X. (2015). The first birth and survival of cub in captivity of critically endangered Malayan pangolin (*Manis javanica*). *Agricultural Science and Technology*, 16, 2322–2323.

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